THE ENDOSPERM OF ANGIOSPERMS

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JOHN M. COULTER

In a recent analysis of all the available testimony in reference to the morphological nature of the endosperm of angiosperms, it seemed clear that certain conclusions might be reached, and the purpose of the present paper is to state them.

It has been assumed that the endosperm must be either gametophytic tissue or sporophytic tissue, and the arguments for each view are familiar. The perplexity has arisen chiefly from the feeling that gametophyte and sporophyte must be subject to rigid definition. When definitions become rigid, ideas become rigid also, and nature is always playing havoc with rigidity. If gametophytes and sporophytes are defined as x and $2x$ structures, respectively, straightway x sporophytes and $2x$ gametophytes are discovered. If sporophytes are defined as structures produced by fertilized eggs, the definition is contradicted by numerous sporophytes that are not the product of fertilization. In this way, every criterion suggested has found its contradiction. It is becoming evident that definitions must be elastic and not rigid, and that general situations rather than definite categories must determine conclusions. We have moved so far beyond the rigid categories of the days of metamorphosis, that it is surprising to find an equal rigidity in the days of alternation of generations.

Without citing an extensive and familiar literature, attention may be called to the various claims that have been made as to the morphological nature of the endosperm of angiosperms.

Ever since the comparative morphology of the vascular groups was uncovered by HOFMEISTER, belief has been general that the endosperm of angiosperms is gametophytic tissue which develops after fertilization. It was easy, even in the days of HOFMEISTER, and much more so now, to obtain from gymnosperms what seems to be abundant confirmation of this claim. Throughout that group there is a distinct tendency to differentiate eggs earlier and earlier

in the ontogeny of the gametophyte. When this differentiation occurs along with the first appearance of tissue after the free nuclear stage (as in *Torreya*), it is clear that the great bulk of endosperm tissue is developed after fertilization. When the differentiation occurs during the free nuclear stage (as in *Gnetum*), it is clear that all the endosperm tissue is developed after fertilization. It was very easy, therefore, to see in the endosperm of angiosperms only belated gametophytic tissue.

When the relation of the polar fusion to endosperm formation began to be appreciated, LE MONNIER (1887) suggested that this fusion is a sexual act, and that therefore the endosperm is sporophytic. This would mean that the embryo and endosperm are twin sporophytes, the latter for some reason not developing the organization of an embryo. This explanation of the polar fusion does not seem to have met with much approval. It is important to note, however, that lack of approval was probably due to the fact that there had developed already a considerable knowledge of the great freedom of nuclear fusions within the embryo sac and within the endosperm. Clearly all such fusions could not be sexual.

With the discovery of "double fertilization," the endosperm problem became conspicuous. One of the nuclei that enters into the triple fusion is plainly a male nucleus; one of the polar nuclei is sister to the egg nucleus, and this was taken to indicate its sexual character; the other polar nucleus has been regarded as vegetative in character. The fusion of an undoubted male cell and an assumed egg was regarded as an act of fertilization, and the product of such a fusion must be a sporophyte. This conclusion as to the nature of the endosperm is inevitable if the triple fusion is to be regarded as involving a sexual fusion.

If the endosperm is a sporophyte, it must be explained why it does not become organized as an embryo, but remains as formless tissue. Miss SARGANT (1900) offered a very ingenious explanation, effectively supported by what seemed to be confirmatory evidence. According to this explanation, the endosperm remains a formless mass of tissue (a "monster") because a vegetative nucleus enters into the fusion and interferes with the legitimate result. This view is attractive, but hardly explains the increasing number of

cases in which the so-called vegetative nucleus does not enter into the fusion, and still the product is only endosperm.

STRASBURGER analyzed the situation, and held to the original interpretation of the endosperm as gametophytic tissue, on the plea that there are two aspects of fertilization, one being fertilization as a stimulus to growth, the other being fertilization as a transmission of hereditary characters. These two aspects he designated respectively vegetative fertilization and generative fertilization. He saw in the result of the triple fusion only a stimulus to growth, resulting merely in tissue, and not a transmission of hereditary characters, which would express itself in an organization. Unfortunately for this view, all the phenomena of xenia are against it, for in such cases it is quite evident that characters of the pollen parent are transmitted to the endosperm by the male nucleus that enters into the triple fusion, but of course there is no sporophytic organization.

Furthermore, the cytological test for the two generations breaks down in this case, as it had in cases of apogamy and apospory, for the endosperm number of chromosomes, in case triple fusion has occurred, is neither x nor $2x$, but at least $3x$. To speak of $3x$ gametophytic tissue is to use some other test than the number of chromosomes. It must not be understood that this in any way affects the general contrast between gametophytes and sporophytes on the basis of chromosome numbers. A generation that follows a reduction division is of necessity an x generation; and one that follows fertilization is a $2x$ generation. But when the reduction division or fertilization does not occur, and still another generation follows, the chromosomes of that generation must become unusual in number, following an unusual situation.

It will be helpful to consider the cases of endosperm formation that do not involve triple fusion. This will enable us to recognize the fact that the origin of endosperm is not necessarily related to the triple fusion, and that we have in endosperm a constant product arising from variable antecedents. It is simple to put such cases into two categories: (1) multiple fusions, and (2) no triple fusion.

(1) The well-known case of *Peperomia* may represent the category of multiple fusions. In the fusion of 8–14 nuclei to form

the "primary endosperm nucleus," we observe an act too miscellaneous to represent anything so definite as fertilization. Moreover, we obtain positive evidence that in the embryo sac there is some condition that favors nuclear fusions, quite apart from what may be called sex attraction.

(2) Cases of no triple fusion, followed by endosperm formation, are numerous. In some instances, there is not even polar fusion, each polar nucleus initiating endosperm formation independently. In other cases, the male nucleus may fuse with either of the polar nuclei, the other nucleus remaining out of the combination, but the result is always the same. When the male nucleus pairs only with the micropylar polar nucleus, one might expect an embryo, if the latter nucleus is really an egg, but endosperm is the result. The increasing number of known angiosperms which are habitually parthenogenetic furnish cases of endosperm formation in the absence of the male nucleus. Of course in such cases the endosperm may be claimed to be parthenogenetic also.

The cases of so-called parthenogenesis among angiosperms illustrate a wider variation in the antecedents of endosperm formation than the mere absence of the male nucleus would seem to indicate. STRASBURGER has called attention to the fact that in the cytologically investigated cases of parthenogenesis there has been no reduction division, and that therefore the parthenogenetic egg is a $2x$ egg, just what it is after normal fertilization. If the failure of reduction results in a $2x$ egg, it must result also in $2x$ synergids, antipodals, and polars; in other words, the gametophyte has throughout the sporophyte number of chromosomes. And still, endosperm formation proceeds as before, when one would be justified in expecting embryo formation by sporophytic budding, a phenomenon very common in the tissues adjacent to the embryo sac. No one questions that the embryo is a sporophyte, whether it is a result of the act of fertilization or not, for it is recognized by its organization. It is pertinent to ask, therefore, why there should be any hesitation in recognizing the endosperm as gametophytic from its lack of organization, no matter how it originates. It is obvious that the constancy of endosperm lies in its structure and not in its origin.

From the facts in hand, the following statements seem to be justified:

(1) Endosperm formation is not dependent upon the presence of a male nucleus.

(2) Endosperm formation is not even dependent upon polar fusion.

(3) Therefore, both of these fusions may be regarded as *supplementary* rather than *determinative*.

(4) Endosperm formation does not even depend upon having been preceded by a reduction division.

(5) The fusions associated with endosperm formation do not represent a definite process, but are miscellaneous in number and order.

(6) The product of such fusions as do occur is merely an undifferentiated tissue, which practically continues the tissue of the gametophyte; that is, it is simply *growth* and not *organization*.

Conclusions

It seems evident that the egg has an organization peculiar to itself. A male cell may fuse with any other cell in the sac, and the result is only endosperm; but occasionally such a fusion (as with a synergid or a polar) results in an embryo. This implies that, for some reason, these ordinarily sterile cells have achieved the organization of eggs. It is this possibility that makes them *potential* eggs; but in the ordinary embryo sac of angiosperms there is only one *actual* egg, which means only one cell capable of being fertilized in any real sense, and therefore capable of producing an embryo.

Conditions in the embryo sac favor fusions of any free nuclei, in any number and of any origin. A male nucleus, perhaps, is more apt to enter into fusions than any other kind.

A male nucleus entering into a fusion may or may not express itself as a carrier of hereditary characters. If it does express itself in this way, it is like injecting certain gamete tendencies into a vegetative fusion; therefore, it is more probable that the male nucleus modifies somewhat the normal product than that the antipodal polar (a vegetative nucleus) modifies a normal product. In

other words, the vegetative fusion is more apt to represent the normal situation than a sexual fusion.

There is no necessary phylogeny of such a performance. It is more a physiological problem to discover the conditions in the embryo sac of angiosperms that favor miscellaneous nuclear fusions.

The final conclusion seems to be that free nuclei within the embryo sac, containing a variable number of chromosomes and reacting to one another in various ways, are in a condition to continue division, and this division is usually carried forward to tissue formation. The whole history of the megaspore and its products justifies us in regarding this tissue, however formed, as gametophytic.

THE UNIVERSITY OF CHICAGO

NOTE.—Since this paper was in type, there has appeared a paper by CAMPBELL on the embryo sac of *Pandanus*,[1] which supplies another illustration of the indefiniteness of the nuclear fusions within the sac. In this case there is an extraordinary development of antipodal tissue before fertilization, and a varying number of free antipodal nuclei fuse with the micropylar polar to form the large primary endosperm nucleus. In some cases two primary endosperm nuclei may be formed by these multiple fusions, and it would seem to make no difference in the result whether the "second male nucleus" fuses with one of them or with neither of them. In either event, it is obviously a vegetative fusion.

[1] Ann. Botany **25**:773–789. *pls. 59, 60. figs. 2.* 1911.